SOME JURASSIC AND CRETACEOUS CRABS (PROSOPONIDAE)

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SOME JURASSIC AND CRETACEOUS CRABS (PROSOPONIDAE)

By THOMAS H. WITHERS

(*With Plates* 15–17)

SYNOPSIS

Further evidence is given of the structure of the early Middle Jurassic Crabs, *Pithonoton richardsoni* and *Prosopon mammillatum*, and the Lower Cretaceous *Mithracites vectensis*; and a new Upper Cretaceous species, *Rathbunopon woodsi*, is described; all belonging to the family Prosoponidae. The additional evidence shown by these Crabs adds much to our knowledge of their structure, as well as to our knowledge of the evolution of the group.

INTRODUCTION

WHEN my paper on the Lower Lias *Eocarcinus praecursor* was written (1932), it was not then possible to compare it adequately with some of the Middle and Upper Jurassic species, for little of those species was known except for the cephalothorax, and what was known often gave a false idea of their structure. Since then I have from time to time paid some attention to several of these forms.

Development, by means of a needle, of the next earliest British Crab, *Pithonoton richardsoni*, added further details of its structure, and the discovery of a second specimen confirmed these findings, for the orbital regions and the hepatic lobe are well preserved.

Development of the holotype and other specimens of *Prosopon mammillatum*, and the discovery in the British Museum collections of a cephalothorax showing the complete left side and of an abdomen, adds considerably to our knowledge of that Crab.

The most striking success was with the Lower Cretaceous (Aptian) *Mithracites vectensis*, for the development of a number of specimens led to the disinterment of the limbs and appendages of this Crab, including one of the last (reduced) pair of legs, and even the maxillae, so that a complete reconstruction could be given (Text-fig. 14).

All this new information adds a great deal to our knowledge of these early Crabs of the family Prosoponidae, as well as to our knowledge of the evolution of the group.

I am indebted to Dr. M. F. Glaessner for kindly reading through some of the manuscript; to Mr. A. G. Brighton and Mr. Henry Woods; to Professor W. F. Whittard; to Mr. D. T. Donovan, who, when he learned that I was working on *Pithonoton richardsoni*, most generously arranged for the second specimen, which he was about to describe, to be sent to me for description; and to Professor H. B. Stenzel for assistance with *Rathbunopon woodsi*.

Tribe BRACHYURA Latreille

Sub-tribe DROMIACEA De Haan

Super-family DROMIIDEA Alcock

Family PROSOPONIDAE von Meyer

Genus ***PITHONOTON*** von Meyer

Genotype. *P. marginatum* von Meyer, 1842: 71. Upper Jurassic (Tithonian): Württemberg.

Diagnosis. Cephalothorax convex transversely and longitudinally. Cervical and branchio-cardiac furrows equally strong. Front broad and straight in typical species. Posterior margin comparatively narrow. Lateral margin weakly developed, never reaching the branchio-cardiac furrow. Sulci for eyes usually well developed.

Pithonoton richardsoni (H. Woodward)

(PLATE 15, FIGS. 1–6; TEXT-FIGS. 1–3)

1907 *Prosopon richardsoni* H. Woodward, p. 80, figs. 1, 2.
1907 *Prosopon richardsoni* H. Woodward: Richardson, p. 82.
1925 *Pithonoton richardsoni* (H. Woodward) Van Straelen, p. 361.
1929 *Pithonoton? richardsoni* (H. Woodward): Glaessner, p. 324.
1933 *Pithonoton? richardsoni* (H. Woodward): Glaessner, p. 181.

DIAGNOSIS. A *Pithonoton* with elongated cephalothorax; orbito-frontal part produced into a wide angle for the rostrum is extended in front to a point; rostrum not downturned as in the genotype *P. marginatum* (Text-figs. 4–6), and in *P. grande* (Text-figs. 7–9), and leaving the front bilobed.

DISTRIBUTION. Middle Jurassic, Bajocian, Inferior Oolite, not found *in situ*, but probably from the Doulting Beds, *Anabacia*-Limestone '*Clypeus*-Grit': Tor Hill, near Wotton-under-Edge, south Cotswolds. Inferior Oolite, *truelli* sub-zone, Upper Coral Bed: 200 yards E. of Walnut Farm, Dundry Hill, Somerset; this is very near the presumed horizon of the holotype.

HOLOTYPE. The cephalothorax figured by H. Woodward in the Geological Department of the British Museum (collected by C. L. Walton and presented by L. Richardson), In. 17026.

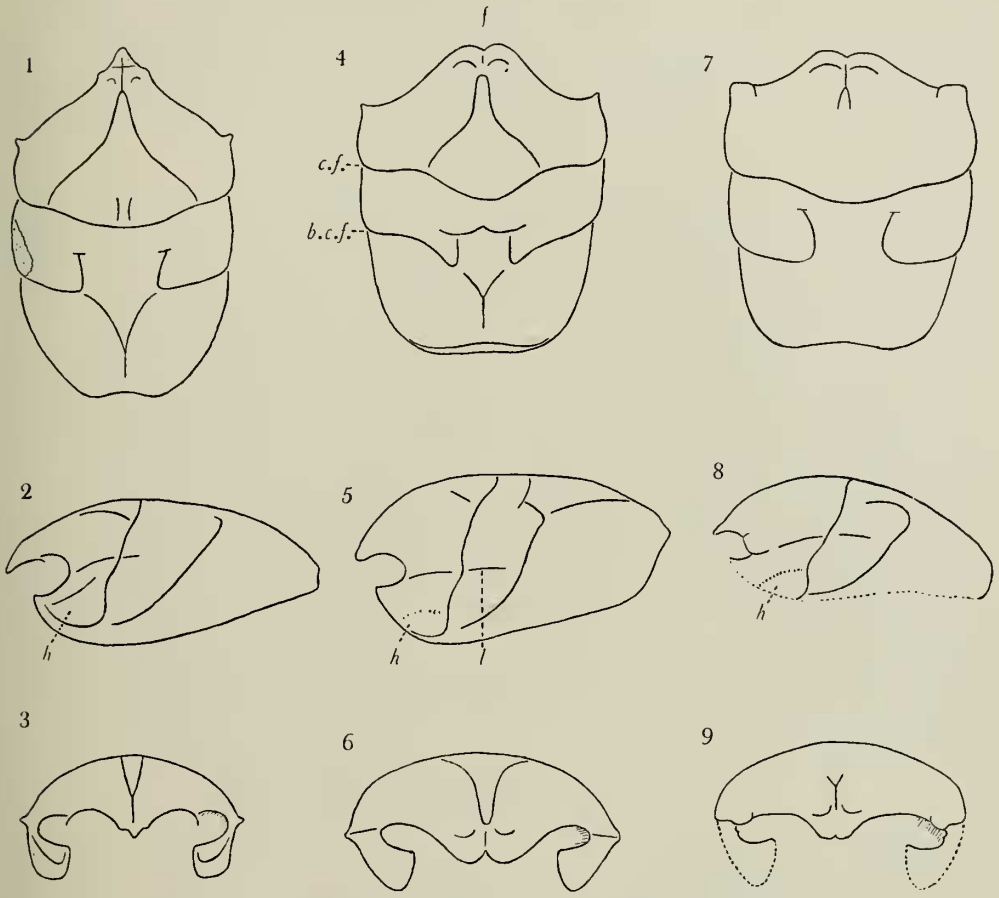
MATERIAL. The holotype, and a cephalothorax in Bristol University (Geol. Dept.), collected by T. R. Fry.

MEASUREMENTS. Cephalothorax (holotype), length 20 mm., breadth 13 mm. Cephalothorax (Bristol Univ.), length 15·8 mm. (incomplete), breadth 12·4 mm.

REMARKS. This is the earliest of the British Oolitic Crabs. H. Woodward first described the species under the genus *Prosopon*, but Van Straelen referred it to the genus *Pithonoton*. There has been some doubt about the generic reference, mainly because of the lack of knowledge of certain characters, and this probably led Glaessner to refer the species to *Pithonoton* with a query. In my opinion, based on the new evidence, it is a primitive form of *Pithonoton*. H. Woodward's figure of the cephalothorax is incorrect in its proportions, especially of the mesogastric lobe, and the several regions were wrongly named by him.

DESCRIPTION. The holotype (Pl. 15, figs. 1–3; Text-fig. 1) is a decorticated cephalothorax, with the shell preserved only at the tip of the rostrum and on the left margin of the branchio-cardiac region. This specimen was developed by me to some extent

to show the fronto-orbital margin, and it was apparent that the orbits must have been shallow (Pl. 15, fig. 2) for the orbital surface is flat; further cleaning showed the



TEXT-FIGS. 1–3. *Pithonoton richardsoni* (H. Woodward).

Fig. 1, outer view, Holotype, Brit. Mus., In. 17026; Fig. 2, side view; Fig. 3, fronto-orbital view; Figs. 2, 3, based on specimen in Bristol University.

TEXT-FIGS. 4–6. *Pithonoton marginatum* von Meyer.

Fig. 4, outer view; Fig. 5, side view; Fig. 6, fronto-orbital view. Based on specimen, Brit. Mus., In. 38253. Upper Jurassic, Tithonian: Stramberg, Moravia.

TEXT-FIGS. 7–9. *Pithonoton grande* von Meyer.

Fig. 7, outer view; Fig. 8, side view; Fig. 9, fronto-orbital view. Based on specimen, Brit. Mus., In. 36846. Upper Jurassic, Tithonian: Stramberg, Moravia.

(*cf.*, cervical furrow; *bcf.*, branchio-cardiac furrow; *f.*, front; *h.*, hepatic lobe; *l.*, lateral margin).

Figs. 1–3, ×2·5 diam.; Figs. 4–6, ×3·0 diam.; Figs. 7–9, ×0·5 diam.

cervical furrow beginning to curve upwards (Pl. 15, fig. 3) to enclose the hepatic lobe, which was badly preserved, and the lateral margin was only barely indicated.

At this stage Mr. D. T. Donovan kindly caused the second-known specimen to be sent to me. This is also a decorticated cephalothorax (Pl. 15, figs. 4–6; Text-figs. 2, 3),

rather worn, and perhaps a little flattened dorsally, judging by the holotype, but the shell is preserved in the orbital regions and along the left side below the lateral margin; the surface is very finely granulated and pitted. Sides of cephalothorax steep and incline inwards. The orbits are comparatively shallow and the lower orbital margin extends anteriorly well beyond the upper orbital margin; there is a slight fissure on the orbital margin, and the outer orbital spine is broken off. Hepatic lobe well developed, situated below the lateral margin, and the cervical furrow curves under it (Pl. 15, fig. 6; Text-fig. 2).

Cephalothorax elongated, a little under one and a half times as long as wide. Front produced into a wide angle, for the rostrum is extended in front, and not sharply downturned; the lateral edges of the rostrum are prominent, for from these edges the surface slopes steeply towards the median longitudinal rostral furrow; on each side of the rostrum near the base there is produced a long, low node. Fronto-orbital margin concave above, and convex below, ending at the prominent outer orbital spine. Antero-lateral margin short and convex. Cervical and branchio-cardiac furrows equally strong, the latter curving downwards nearly to the posterior margin. Mesobranchial lobe wide, more than twice the width of the gastric region on each side, and well defined by a furrow on each side; there is a slight indication of a short median longitudinal depression at the base. Urogastric furrows short, and not deeply defined. Posterior margin rather broken, but probably about half the greatest width of the cephalothorax. Orbits comparatively shallow, divided off on the inner side by the frontal margin which curves downwards, reminding one of this feature which is so well shown in specimens of *Dromiopsis* (Dynomenidae); lower orbital margin extending well beyond the upper orbital margin. Lateral margin weakly developed anteriorly, and dying out less than half-way to the branchio-cardiac furrow. There seems to be no justification for the four tubercles on the 'cardiac' region seen in Woodward's figure.

Genus ***PROSOPON*** von Meyer

Genotype *P. tuberosum* von Meyer, 1840: 21. Lower Cretaceous, Neocomian: Boucherans (Jura), France.

Diagnosis. Cephalothorax strongly vaulted. Branchio-cardiac furrow more strongly developed than cervical furrow. Front narrow. Posterior margin broad. Lateral margin not developed. Sulci for eyes absent.

Prosopon mammillatum H. Woodward

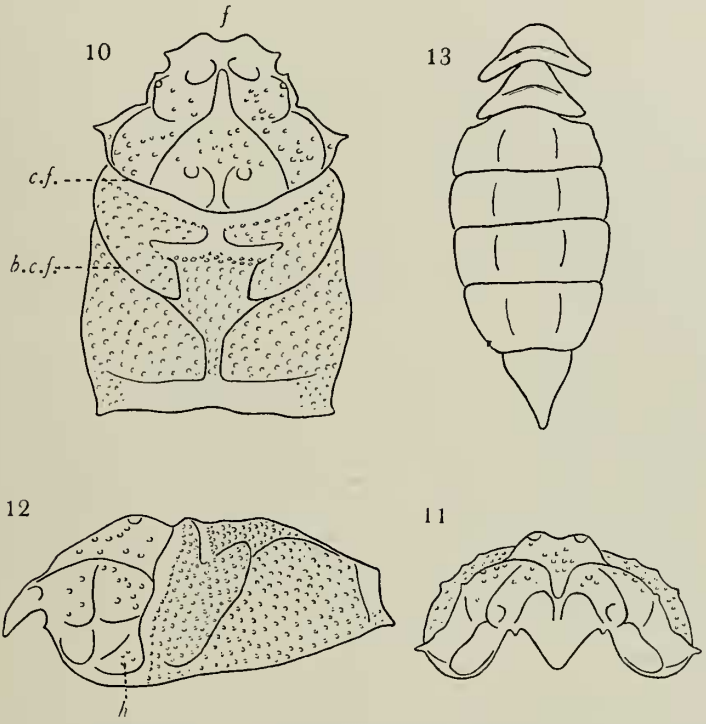
(Plate 16, figs. 1–4; Text-figs. 10–13)

1868 *Prosopon mammillatum* H. Woodward, p. 3, pl. 1, figs. 2, 2*a*.
1877 *Prosopon mammillatum* H. Woodward: H. Woodward, p. 6.
1925 *Avihomola mammillata* (H. Woodward) Van Straelen, p. 340.
1929 *Protocarcinus mammillatus* (H. Woodward) Glaessner, p. 349.
1933 *Prosopon mammillatum* H. Woodward: Glaessner, p. 180.

Diagnosis. A *Prosopon* with the lobes of the cephalothorax strongly protuberant,

a prominent spine on each hepatic lobe, and two large spines towards the base of the mesogastric lobe; surface coarsely granulated.

Remarks. *Prosopon mammillatum* was described as long ago as 1868, and since that date nothing further has been added to our knowledge of it. Van Straelen (1925: 340) referred the species to his genus *Avihomola*, which is a synonym of Woodward's genus *Protocarcinus* (1865). Glaessner (1929: 349) referred the species



Text-figs. 10–13. *Prosopon mammillatum* H. Woodward.

Fig. 10, outer view; Fig. 11, fronto-orbital view; Fig. 12, side view; Fig. 13, abdomen. (*c.f.*, cervical furrow; *b.c.f.*, branchio-cardiac furrow; *f.*, front; *h.*, hepatic lobe.) Figs. 10–12 × 1·5 diam.; Fig. 13, nat. size.

to *Protocarcinus*, and later (1933: 180) to the genus *Prosopon*. It has not been possible for me to see the genotype of *Prosopon* (*P. tuberosum*).

Distribution. Middle Jurassic, Middle Bathonian, Great Oolite, Stonesfield Slate: Stonesfield, Oxfordshire.

Holotype. A cephalothorax in the Sedgwick Museum, Cambridge, B. 2719.

Material. In the British Museum are two examples of the cephalothorax (44291, Morris colln.; 59664, Hon. R. Marsham colln.); the left half of a cephalothorax, In. 28821; the left branchial part of the largest-known cephalothorax (I. 269, Sir P. de M. G. Egerton colln.); three fragments of the cephalothorax (59664, I. 3289, In. 28822), and a complete female abdomen (I. 3048, P. B. Brodie, *ex* Stutchbury colln.)

Measurements. Holotype, length, including the rostrum, 34 mm.; breadth 24 mm. Specimen In. 28821, Pl 16, fig. 2, length, including rostrum, but slightly incomplete posteriorly, 44 mm. Specimen I. 269 measures 31·5 mm. from the cervical furrow to the posterior margin, so the complete cephalothorax would measure about 55 mm. Abdomen, length 52·5 mm.

Description. The holotype of *Prosopon mammillatum* is a cephalothorax showing the dorsal surface and retaining its original convexity. Woodward's figure shows two spines on each side, one apparently projecting from the protogastric lobe, and the other from the frontal part of the cephalothorax. Actually, those on the left side were not seen in the specimen, but the right posterior spine is preserved and is produced from the hepatic lobe. Careful development of the anterior part of the holotype has exposed two comparatively large epigastric lobes, followed by a wide, tongue-shaped, and strongly downturned rostrum. Woodward's figure showing a two-spined rostrum is therefore wholly inaccurate. At the base of the rostrum, on the left side, a wide, flattened, triangular spine has now been exposed, but that on the right side is broken off, and below its level lies what may or may not be the basal part of an eye-stalk. It was on this latter that Woodward may have based his anterior spines.

Two examples of the cephalothorax in the British Museum (Nos. 44291, 59664) show only the dorsal surface, and although they are a little more flattened than the holotype, they exceed it in size. More important is a cephalothorax (In. 28821) much larger than those above, preserved as a cast and showing little more than the left side, except that the rostrum is entire, and nearly all of the mesogastric lobe is preserved. Its importance lies in the fact that it is the only known specimen which shows the whole of the antero-lateral and branchial margins, and this not only allows us to see how cylindrical the cephalothorax really is, but more important still, the direction of the cervical and branchio-cardiac furrows, and the hepatic lobe.

In addition there is a female abdomen which has been cleaned to show all the segments; it is not attached to any cephalothorax, but since *Prosopon mammillatum* is the only crab known to occur in the Stonesfield Slate, and is known by the remains of at least eight examples of the cephalothorax, and considering their correspondence in size to this abdomen, there can be little doubt that it belongs to the same species. The abdomen has a length of 52·5 mm., and must have belonged to an individual exceeding in length the largest known cephalothorax. *Prosopon mammillatum* is therefore the largest of the known Upper Jurassic Crabs, even larger than the Lower Liassic *Eocarcinus*, and as will be shown later, throws further light on the phylogeny of the Brachyura.

Cephalothorax cylindrical, with steep sides; almost one and a half times as long as wide, widest at its posterior third, convergent in front; very strongly convex transversely; moderately convex longitudinally. Rostrum comparatively wide, tongue-shaped, somewhat excavated, strongly downturned in front, with a prominent, flattened, and triangular spine on each side at the base, just in front of the epigastric lobes. These wide basal spines evidently served for the protection of the eye-stalk. No sulci for eyes. Regions and furrows distinctly marked, the regional lobes very prominently raised. Cervical furrow strongly marked, continuous, wide and deep,

obtusely V-shaped. Branchio-cardiac furrow well defined, but not so wide and deep as the cervical, and near the antero-lateral margin is directed slightly backwards and abruptly forwards to meet the cervical furrow; above this junction is the large hepatic lobe. Surface ornamented with fairly coarse granules. Two comparatively large epigastric lobes are seen behind the base of the rostrum. On the swollen mesogastric lobe, two large prominences, evidently the bases of broken-off spines, are situated at the wide posterior end, and a small prominence is situated near the base of the narrow triangular process; the remainder of the lobe has several irregularly placed tubercles. Hepatic lobe swollen and prominent and divided transversely and obliquely by a ridge into two almost equal parts, the outer part having a prominent spine on its outer margin, well seen in dorsal view. Above the hepatic lobe is a smaller lobe bounded above by the orbital margin. Protogastric lobe rounded and prominent, bounded posteriorly by the cervical furrow. Urogastric lobe with two comparatively small tubercles separated by a deep, wide depression, and the cardiac lobe is rather swollen, with deep lateral furrows, and bears two small tubercles near the base. Antero-branchial lobe with a deep depression close to the urogastric lobe, and bounded laterally by the cardiac furrow.

Abdomen comparatively broad (length 52·5 mm.; greatest breadth, at the fourth segment, 22·5 mm.), with seven separate segments. The first two segments are comparatively long and narrow, divided transversely by a groove across the middle, strongly excavated at the sides, so that the basal angles are acute and free; the third to sixth segments increase in height, the sixth being the longest, and their lateral margins form a continuous curved line, or in other words the lateral margins are not free; the seventh segment is acutely triangular. There is some convexity of the surface down the middle of the third to sixth segments. The excavation of the first two segments shows that the abdomen was not entirely folded under the cephalothorax, and indicates that the last pair of legs were reduced and carried elevated on the back.

Genus ***RATHBUNOPON*** Stenzel

Genotype *R. polyakron* Stenzel, 1945: 450. Lower Cenomanian, Comanche Series, Washita Group, Grayson Marl: northwestern Austin, Travis Co., Texas.

Diagnosis (after Stenzel). Carapace ovoid in outline, slightly longer than wide; fronto-orbital width about three-quarters of width. Frontal rostrum short, barely projecting, triangular, and with a median groove. Orbits well defined, about twice as wide as high, with two notches on the upper margin and a projecting dentiform tubercle on the lower margin. Lateral margins of carapace poorly defined. Cervical and other grooves deep. Urogastric and metagastric regions well separated and of the shape of transverse bars. Mesobranchial region bilobed toward the cardian grooves. Metabranchial regions large, confluent or nearly confluent at midline.

Rathbunopon woodsi n. sp.

(Plate 16, figs. 5, 6)

Diagnosis. A *Rathbunopon* like *R. polyakron* but with the cephalothorax more strongly convex transversely, orbito-frontal part more constricted; rostrum nar-

rower, slightly longer, with straighter sides; cardiac lobe longer, with posterior end more sharply pointed, and with postero-lateral delineation of the lobe less convexly curved; orbital margin with two well-defined tubercles.

Distribution. Cenomanian, upper *varians* zone (Meyer's Bed 12): Beer Head, Devonshire.

Holotype. A decorticated cephalothorax in the Sedgwick Museum, Cambridge (Meyer colln.), B. 50,779.

Measurements. Length, including rostrum, 18·8 mm.; breadth, 15·3 mm.; fronto-orbital breadth, 9·0 mm.

Description. Cephalothorax sub-ovate, a little longer than wide, much convergent anteriorly, widest at its posterior third, strongly convex transversely and moderately convex longitudinally. Front produced into a comparatively narrow tongue-shaped rostrum, which is strongly downturned, its edges prominently raised; rostrum with a slight median longitudinal furrow, and near the middle of each side is produced into a long, low tubercle. Outer orbital spine prominent. Orbital margin less than the width of the base of the rostrum, with two well-defined tubercles, close together, and divided by a fissure. Orbits large and deep. Antero-lateral margins strongly convergent, with a large tubercle on the outer margin of the mesobranchial lobe taking up almost the whole of the space between the cervical and branchio-cardiac furrows; postero-lateral margins protuberant; posterior margin moderately convex, much wider than the fronto-orbital margin, with a narrow, raised marginal rim, bounded above by a very wide depression. No definite lateral margin developed.

Since the surface of the shell is only preserved in places, the specimen is almost in the form of an internal cast, but the surface must either have been smooth or only very finely granulated. Regions and furrows distinctly marked. Branchio-cardiac furrow very deep. Cervical furrow well developed above the mesobranchial region; it then extends round the top of, and to below, the large outer mesobranchial tubercle, and is then directed forwards at the branchio-cardiac furrow to enclose the low hepatic lobe (seen only in side view) in front of it. A small but prominent tubercle is situated on each epigastric lobe, and each tubercle is separated by a wide space from two close tubercles on the upper orbital margin; the two latter are separated by a deep fissure. A large tubercle is placed on each protogastric lobe; a triangle of three tubercles on the mesogastric lobe, which is fairly well defined by lateral furrows. Mesobranchial lobe bilobed towards the gastric region, the upper limb forming a large boss, and the lower limb slender; near the outer end of the lower limb there is a somewhat transverse depression. A large outwardly directed tubercle is situated on the outer margin of the mesobranchial lobe. Metagastric bar a little longer than the urogastric bar, and confluent with the mesobranchial boss. Urogastric bar separated from the metagastric bar by a fairly deep furrow, and by a deeper furrow from the cardiac lobe. Metabranchial region devoid of tubercles. Cardiac lobe is in the form of an inverted and somewhat acute triangle, with no trace of pits, and bounded by deep lateral furrows. Intestinal lobe small, somewhat triangular, and situated almost wholly in the wide depression above the posterior margin.

In the Geological Department of the British Museum there is a specimen (No. 24657) represented by a worn internal cast (Pl. 16, fig. 7) from the Albian (Gault)

of Folkestone, Kent. It closely agrees with the above species, but it appears to differ in that the metagastric bar is not apparent, and the cardiac lobe is slightly larger. Nothing more can be done with such an ill-preserved specimen.

Comparison with other species. This species is very close to the genotype *Rathbunopon polyakron*, but since the holotype of that species is a cephalothorax with well-preserved surface, and the present species, *R. woodsi*, is founded on a decorticated, but uncrushed specimen, the differences may be partly, but not wholly, illusory. *R. woodsi* has the cephalothorax more strongly convex transversely, and the fronto-orbital part more constricted; rostrum narrower, slightly longer, with straighter sides; cardiac lobe longer, with posterior end more sharply pointed, the postero-lateral delineation of the lobe less convexly curved, and no trace of pits; orbital margin with two well-defined tubercles, but *R. polyakron* has these same tubercles feebly indicated; metagastric bar confluent with the mesobranchial boss, but in *R. polyakron* the ends of the metagastric bar are pinched off from the mesobranchial boss, and the groove separating the urogastric bar from the mesobranchial region is deeper; branchio-cardiac furrow with more definite upward sweep; mesobranchial lobe bilobed, but with the lower limb longer and more slender; intestinal lobe placed in a more posterior position; metagastric lobe slightly longer than the urogastric lobe; large tubercle on outer margin of mesobranchial region more prominent and more widely spaced from the protogastric tubercle.

Genus ***MITHRACITES*** Gould

Diagnosis. A Prosoponid with the cephalothorax sub-circular, moderately convex transversely and longitudinally, posterior margin wide and convex. Lateral margin distinctly developed. Front produced into a wide tongue-shaped rostrum, slightly downturned. Sulci for eyes wide, somewhat rounded and shallow, the sub-orbital margin produced well beyond the supra-orbital margin. Last pair of pereiopods reduced and elevated on the back.

Remarks. This monotypic genus was first described by Gould (1859) and based on the species *M. vectensis* Gould, represented only by a poorly preserved cephalothorax. Two similar specimens were figured by Bell (1863), and Carter (1898) added to Bell's description. Woodward (1874) mentions more complete specimens which were not subsequently described.

The systematic position of this Crab has been rather doubtful, and this is no doubt due to the poor preservation of the specimens so far figured. Some twenty-two specimens in the Geological Department of the British Museum have been prepared by me—some of these were probably those mentioned by Woodward—and from these specimens it is now possible to make known its structure, and to give a reconstruction of the entire crab.

Mithracites vectensis Gould

(Plate 17, figs. 1–5; Text-fig. 14)

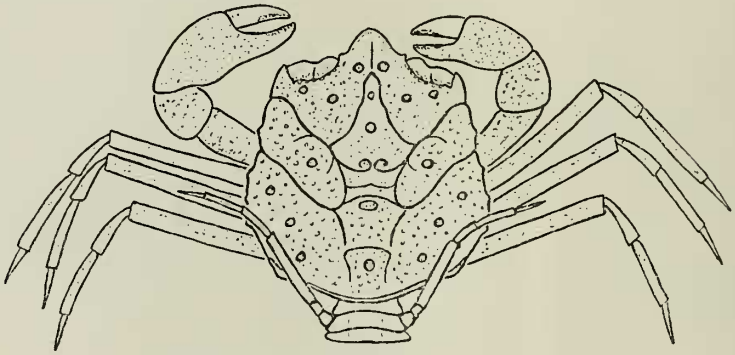
1859 *Mithracites vectensis* Gould, p. 237, figs. 1–3.
1863 *Mithracites vectensis* Gould: Bell, p. 1, figs. 2, 3.
1874 *Mithracites vectensis* Gould: H. Woodward, p. 307.

1877 *Mithracites vectensis* Gould: H. Woodward, p. 14.
1898 *Mithracites vectensis* Gould: Carter, p. 32.
1929 *Mithracites vectensis* Gould: Glaessner, p. 259.

DIAGNOSIS. Same as for the genus.

DISTRIBUTION. Lower Cretaceous (Aptian), *deshayesi* zone, Lower Greensand: Atherfield, Isle of Wight.

GENOHOLOTYPE. A cephalothorax in the Geol. Dept. of the British Museum (presented by J. Middleton), In. 28837. The original of Bell's fig. 2 (59771) and fig. 3 (In. 28841) are in the same collection.



TEXT-FIG. 14. *Mithracites vectensis* Gould.
Reconstruction, based on specimens figured Pl. 17, figs. 1–5. ×1·5 diam.

MATERIAL. In addition to the above three specimens, there are nineteen specimens in the same collection in varying states of preservation.

DESCRIPTION. Cephalothorax sub-circular, and when uncrushed and including the rostrum, very little longer than wide, widest at its posterior third; moderately convex transversely, and a little more strongly longitudinally. Front produced into a comparatively wide tongue-shaped rostrum, which is a little downturned; the edge is raised and prominent, especially anteriorly, and there is a median longitudinal depression, and a small low spine on each side at the base of the rostrum. Orbital margin concave, wider than the base of the rostrum, and partly defined by a ridge of small tubercles extending from the base of the rostrum and ending at a wide shallow notch near the outer orbital spine. Outer orbital spine prominent. From the supra-orbital margin the sulci for the eyes extend downwards and outwards well beyond the supra-orbital margin; the sulci for the eyes are therefore wide and shallow, somewhat rounded, divided by an oblique furrow into two halves and ending in a notch at the sub-orbital margin (Pl. 17, fig. 1 *b*). Antero-lateral margins very slightly convergent, with a single small tubercle near the branchio-cardiac furrow; postero-lateral margins strongly convex, protuberant, with a row of three tubercles on the anterior two-thirds; posterior margin slightly convex, comparatively wide, with a narrow raised marginal rim. Lateral margins well developed.

Regions and furrows distinctly marked. Surface ornamented with fine irregularly spaced tubercles, which on the larger prominences are closely set. Of the large

tubercles, one is situated on each epigastric lobe immediately behind the base of the rostrum, and two on each protogastric lobe; a single small tubercle is placed on the triangular process of the mesogastric lobe, followed behind by a large tubercle; two tubercles, separated by a longitudinal depression, are placed at the base of the mesogastric lobe; a large tubercle is placed on the cardiac lobe, and the intestinal lobe forms a large rounded prominence separated from the cardiac lobe by a deep and curved furrow; a single tubercle is situated on each antero-branchial lobe, nearer to the cardiac furrow, and a curved longitudinal line of three tubercles is seen on the postero-branchial lobe.

Abdomen not entirely folded under the cephalothorax, broad in both sexes, the segments distinct; female with the seventh segment (telson) almost flat and obtusely triangular, nearly twice as wide as long, but in the male this segment is deeply excavated towards its base and is almost as long as wide. There are no intercalated plates (uropods) between the sixth segment and the telson such as are seen in the family Dromiidae.

Ischium of third maxillipede with a deep oblique longitudinal groove extending from the middle of the anterior margin to near the base of the outer margin; exopodite slender, with a median longitudinal carina. Details of antennary regions and buccal-frame are seen in the specimen figured Pl. 17, figs. 3 *b*, *c*; the buccal-frame and mandibles are seen in the specimen figured Pl. 17, fig. 4.

Chelipeds (1st pereiopods) slightly unequal, the left a little larger than the right in specimen In. 28832 (Pl. 17, fig. 3), finely granulated, merus short and stout; carpus short and rounded; propodus strongly convex outwardly, with the palm flattened. Fingers little more than half the length of the hand, with a single large, low tooth.

Pereiopods (2nd–4th) flattened laterally, with the dactylus slender and pointed; 5th and last pereiopod much reduced, about one-third the length of the others, and carried elevated on the back.

PHYLOGENY

The Lower Lias *Eocarcinus praecursor* is by far the geologically oldest crab and is more complete than any other Jurassic crab. Although crabs have been found in the succeeding Bajocian, Bathonian, and Tithonian rocks, they are, except for the Upper Bathonian *Prosopon auduini* (Eudes-Deslongchamps), known only by their cephalothorax. In most species the cephalothorax shows only the dorsal surface, and since in some the fronto-orbital part is incompletely exposed, the published figures often give a false idea of their real structure. Many of the Jurassic species require study and redescription.

The next earliest form is *Pithonoton*, and crabs of this genus have a simple cephalothorax not very unlike that of *Eocarcinus*. *Pithonoton richardsoni* (Text-fig. 1), from the Bajocian (Inferior Oolite), has a comparatively narrow cephalothorax with the rostrum extended in front, the mesogastric lobe completely developed, and a narrow posterior margin. In the later Tithonian forms, the genotype *P. marginatum* (Text-fig. 4) and *P. grande* (Text-fig. 7), the cephalothorax is more foreshortened, the rostrum downturned so that it is not seen in dorsal view, the front widely bilobed,

and the posterior margin wider. *P. marginatum* is nearer to *P. richardsoni*, for the mesogastric lobe is completely developed, although not so wide, but in *P. grande* the mesogastric lobe is only indicated by the acutely angular anterior process, and is therefore not even so far developed as it is in *Eocarcinus*. Both in *Eocarcinus* and *Pithonoton* there is a well-developed hepatic lobe in front of the cervical furrow under the lateral margin. But what distinguishes *Pithonoton* is the development of a lateral margin, although it does not extend as far as the branchio-cardiac furrow, and the development of sulci for the eyes, which are deeper in the later Tithonian forms than in the earlier Bajocian *Pithonoton richardsoni*.

The cephalothorax of the Middle Bathonian *Prosopon mammillatum* shows agreement with the more simple *Eocarcinus praecursor* in the absence of sulci for the eyes, the absence of a lateral margin, in the direction of the cervical and branchio-cardiac furrows, and in the presence of the hepatic lobe and a lobe behind what would be the orbital region. In its remaining characters *P. mammillatum* is more advanced, for while in *Eocarcinus* the mesogastric lobe is indicated only by the end of the triangular process behind the rostrum, and by the two short grooves emerging from the cervical furrow, this same lobe is fully developed in *P. mammillatum*, as also are the epigastric and protogastric lobes, and there is a well-developed rostrum.

While some modification has therefore taken place in the cephalothorax of *Prosopon mammillatum* in the direction of the formation of regional lobes, much more rapid and not altogether unexpected development is shown by the abdomen, for it has already the structure of a typical crab. There are no pleura as in *Eocarcinus praecursor*, except in the first two segments, for the outer margins of the third to sixth segments form a continuous line, and the last segment, the telson, is small and acutely angular. Unlike *Eocarcinus*, which has the abdomen extending posteriorly, the abdomen must have to some extent been folded under the cephalothorax, although the lateral excavation of the first two segments shows that these must have been seen in dorsal view, and the last pair of legs were evidently reduced and folded on the back. There are no intercolated plates between the sixth segment and the telson, such as are seen in the later family Dromiidae.

In *Eocarcinus* the last two pairs of legs were reduced and carried on the back. That only the last pair were reduced in *Prosopon* was deduced from the form of the first two segments of the abdomen in *P. mammillatum*, but in the Upper Bathonian *P. auduini* (Eudes-Deslongchamps) and in the Lower Cretaceous (Neocomian) *P. gignouxi* Van Straelen (1928), the 2nd–4th pereiopods appear to be well developed, so that only the last pair could have been reduced.

In short, while *Eocarcinus* shows clearly its derivation from a macrurous stock—the Pemphicoida—*Prosopon* and *Pithonoton* show in turn the derivation of the Prosoponidae from an *Eocarcinus* stock.

Mithracites vectensis, from the Lower Cretaceous (Aptian), as now revealed by its structure, leaves no doubt that it belongs to the family Prosoponidae. *Mithracites* may be regarded as a form derived from the *Prosopon-Pithonoton* stock, for it agrees with both genera in many of its characters. It differs from both genera, which have a more cylindrical cephalothorax with steep sides and concave posterior margin, for the cephalothorax of *Mithracites* is much foreshortened, even sub-circular, it has

a wide convex posterior margin, well-defined lateral margins, and the rostrum is not so much downturned and can be seen in dorsal view. It agrees more with *Prosopon*, especially the Middle Bathonian *P. mammillatum*, in the development of the various regions, but the sulci for the eyes are not developed in *Prosopon*; in *Mithracites* the sulci for the eyes are wide and shallow. Although in the Upper Bathonian *P. auduini* (see Withers, 1932, pl. 10, fig. 3) there is no orbital margin developed, there are very slight hollows developed in the orbital region, and these may represent incipient sulci. In the Tithonian species of *Pithonoton* deep sulci for the eyes are present, but in the earlier Bajocian species *Pithonoton richardsoni* the sulci for the eyes are comparatively shallow. In *Prosopon* a lateral margin is not developed; in *Pithonoton* it is only weakly developed anteriorly, for it does not extend as far back as the branchiocardiac furrow; and in *Mithracites* a lateral margin is well developed.

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PLATE 15

Pithonoton richardsoni (H. Woodward)

Bajocian, Inferior Oolite, not found *in situ*, but probably from Doulting Beds, *Anabacia* Limestone (= *Clypeus* Grit): Tor Hill, near Wotton-under-Edge, south Cotswolds

FIG. 1. Cephalothorax (holotype). Dorsal view. Brit. Mus., In. 17026.
FIG. 2. Front view of same.
FIG. 3. Side view of same.

Bajocian, Inferior Oolite, *truelli* sub-zone, Upper Coral Bed: 200 yds. E. of Walnut Farm, Dundry, Somerset.

FIG. 4. Cephalothorax. Dorsal view. Bristol Univ. (Geol. Dept.).
FIG. 5. Front view of same.
FIG. 6. Side view of same.

[Figs. 1–6 × 2 diam. Photographs taken by M. G. Sawyers.]

1

4

2

5

3

6

PITHONOTON RICHARDSONI

PLATE 16

Prosopon mammillatum H. Woodward

Middle Bathonian, Great Oolite, Stonesfield Slate:
Stonesfield, Oxfordshire

FIG. 1. Cephalothorax. Dorsal view. Holotype. Sedgwick Museum, Cambridge, B. 2719.

FIG. 2. Cephalothorax (left half). Brit. Mus., In. 28821.

FIG. 3. Cephalothorax (branchial part of left side). Brit. Mus., I. 269.

FIG. 4. Abdomen (female) of large individual. Brit. Mus., I. 3048.

(Figs. 1–4, nat. size.)

Rathbunopon woodsi n.sp.

Cenomanian, upper *varians* zone (Meyer's Bed 12):
Beer Head, Devonshire

FIG. 5. Cephalothorax (internal cast). Holotype. × 1·5 diam. Sedgwick Museum, Cambridge, B. 50,779.

FIG. 6. Front view of same.

Albian, Gault: Folkestone, Kent.

FIG. 7. Cephalothorax (worn internal cast). × 3 diam. Brit. Mus., 24657.

[Photographs taken by H. G. Herring.]

1

2

6

7

5

4

3

PROSOPON MAMMILLATUM. (FIGS. 1-4) *AND* RATHBUNOPON WOODSI (FIGS. 5-7)

PLATE 17

Mithracites vectensis Gould

Lower Greensand (Lower Aptian, *deshayesi* zone): Atherfield, Isle of Wight

FIG. 1. *a*, Cephalothorax with left cheliped (1st pereiopod); *b*, front view of same showing rostrum and orbital regions; *c*, chela (left) of same. In. 28835.

FIG. 2. *a*, Individual (? female) with right cheliped, and abdomen showing 2nd–5th segments; *b*, part of under surface showing 6th and 7th segments of abdomen (for comparison with male, Fig. 3 *c*). In. 28828.

FIG. 3. *a*, Individual (? male) showing cephalothorax with right eye-stalk, both chelipeds (1st pereiopods), 2nd and 3rd pereiopods (on right side), and 4th pereiopod (on left side); *b*, front view of same showing orbital regions, right eye-stalk, and antennary region; *c*, under surface of same showing buccal-frame, both chelipeds, 4th–7th segments of abdomen, 3rd maxillipede, and 2nd–4th pereiopods; *d*, posterior view of same showing margin, bases of 4th pereiopods, and 2nd segment of abdomen (for comparison with ? female, Fig. 2 *a*). In. 28832.

FIG. 4. Cephalothorax showing under surface with mouth-frame, maxillae, and part of sternum. In 28836.

FIG. 5. *a*, Individual (? male) showing abdomen (2nd–7th segments), 3rd and 4th pereiopods (complete) of right side, and bases of 2nd–4th pereiopods of left side; *b*, dorsal surface of same showing reduced 5th or last pereiopod, elevated on the back. In 25770.

[All figures × 1·5 diam. All the specimens are in the Geological Department of the British Museum. Photographs taken by H. G. Herring.]